Distribution, Density, and Biomass of Introduced Small Mammals in the Southern Mariana Islands[1]

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Abstract: Although it is generally accepted that introduced small mammals have detrimental effects on island ecology, our understanding of these effects is frequently limited by incomplete knowledge of small mammal distribution, density, and biomass. Such information is especially critical in the Mariana Islands, where small mammal density is inversely related to effectiveness of Brown Tree Snake (*Boiga irregularis*) control tools, such as mouse-attractant traps. We used mark-recapture sampling to determine introduced small mammal distribution, density, and biomass in the major habitats of Guam, Rota, Saipan, and Tinian, including grassland, *Leucaena* forest, and native limestone forest. Of the five species captured, *Rattus diardii* (sensu Robins et al. 2007) was most common across habitats and islands. In contrast, *Mus musculus* was rarely captured at forested sites, *Suncus murinus* was not captured on Rota, and *R. exulans* and *R. norvegicus* captures were uncommon. Modeling indicated that neophobia, island, sex, reproductive status, and rain amount influenced *R. diardii* capture probability, whereas time, island, and capture heterogeneity influenced *S. murinus* and *M. musculus* capture probability. Density and biomass were much greater on Rota, Saipan, and Tinian than on Guam, most likely a result of Brown Tree Snake predation pressure on the latter island. *Rattus diardii* and *M. musculus* density and biomass were greatest in grassland, whereas *S. murinus* density and biomass were greatest in *Leucaena* forest. The high densities documented during this research suggest that introduced small mammals (especially *R. diardii*) are impacting abundance and diversity of the native fauna and flora of the Mariana Islands. Further, Brown Tree Snake control and management tools that rely on mouse attractants will be less effective on Rota, Saipan, and Tinian than on Guam. If the Brown Tree Snake becomes established on these islands, high-density introduced small mammal populations will likely facilitate and support a high-density Brown Tree Snake population, even as native species are reduced or extirpated.

Introduced small mammals, especially *Rattus* species, often have detrimental effects on island ecology. Direct effects include competition with, or predation on, amphibian, avian, invertebrate, mammalian, plant, and reptilian species, often resulting in population declines or even extirpation (reviewed in Atkinson 1985, Towns et al. 2006, Jones et al. 2008). Less apparent indirect effects include disruption of island trophic systems (Fritts and Rodda 1998, Towns 1999) and nutrient cycling (Fukami et al. 2006), modification of vegetative community structure and successional patterns (Campbell and Atkinson 2002), and creation of novel vectors and reservoirs for diseases and parasites (Pickering and Norris 1996, Chanteau et al. 1998).

Despite this growing body of evidence, our understanding of the effects of introduced small mammals on island ecology is far from complete. To provide a framework

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for future research, Parker et al. (1999) proposed that three factors determine the impact of introduced species on island ecosystems: their distribution, density or biomass, and effect per individual or unit biomass. Those authors suggested that distribution, density, and biomass are easier to quantify than the per-individual or unit biomass effect of introduced species (Parker et al. 1999). Although this claim is valid from a procedural standpoint, in practice the distribution, density, and biomass of introduced small mammals are poorly understood on many islands. This lack of knowledge is especially surprising for well-studied island systems, such as the Mariana Islands, infamous for the introduced Brown Tree Snake (*Boiga irregularis* [Savidge 1987, Fritts and Rodda 1998]). In spite of considerable research effort associated with controlling the Brown Tree Snake on Guam and preventing its spread to other vulnerable locations (Colvin et al. 2005), relatively little is known about introduced small mammals in the Mariana Islands, limiting our ability to investigate their effect on both the ecology of the Mariana Islands and Brown Tree Snake control and management.

Based on studies elsewhere in the Pacific, the Mariana Islands have a suite of native species potentially vulnerable to introduced small mammals, including bats, birds, invertebrates, plants, and reptiles, yet putative impacts have not been evaluated in the Mariana Islands despite the large proportion of species declining or endangered without a clear cause (e.g., Fancy and Snetsinger 2001, U.S. Fish and Wildlife Service 2005). Attempts to use historic data to investigate introduced small mammal distribution, density, and biomass in the Mariana Islands are complicated by the common reliance on nonrigorous sampling techniques, such as low sampling effort and convenience sampling (Anderson 2001, 2003), and the frequent dependence on indices of density. As a result, retrospective comparisons across sites, habitats, or islands require unrealistic assumptions about the equality of capture probability across space and time (Anderson 2001, 2003). Thus, our objectives were to: (1) determine the distribution of introduced small mammals across the major habitats of Guam and the nearby islands of Rota, Saipan, and Tinian, and (2) generate robust estimates of density and biomass using rigorous and repeatable mark-recapture livetrapping methods.

MATERIALS AND METHODS

Study Area

The Mariana Islands consist of 15 islands arrayed in a north-south arc between 13 and 21° N and 144 and 146° E. The marine tropical climate of the Mariana Islands results in minimal seasonal temperature variation, with monthly averages ranging from 24°C to 27°C (Mueller-Dombois and Fosberg 1998). Precipitation is seasonal, with a rainy season from July to October, and averages 2,000–2,500 mm/yr (Mueller-Dombois and Fosberg 1998).

Our study occurred on the islands of Guam, Rota, Saipan, and Tinian. Geologically, these islands consist of upraised coral plateaus and weathered volcanic substrates. The dominant native vegetative community of the coral substrate is limestone forest, which is most common and least disturbed on Rota (Falanruw et al. 1989). These forests have highly variable structure and species composition, primarily as a function of slope, aspect, and elevation as well as the frequency and extent of typhoon damage and human disturbance (Mueller-Dombois and Fosberg 1998). Common limestone forest species include *Aglaia mariannensis*, *Artocarpus mariannensis*, *Cycas circinalis*, *Cynometra ramiflora*, *Elaeocarpus joga*, *Ficus prolixa*, *Guamia mariannae*, *Ochrosia mariannensis*, *Pandanus dubius* and *P. tectorius*, *Pisonia grandis*, and *Premna obtusifolia* (Mueller-Dombois and Fosberg 1998). Many disturbed areas have been colonized by the introduced leguminous tree *Leucaena leucocephala*, especially on Guam, Saipan, and Tinian. This species often exists in nearly monotypic stands but is also found in association with *Flagellaria indica*, *Hibiscus tiliaceus*, *Nephrolepis biserrata* and *N. hirsutula*, and *Triphasia trifolia* (Mueller-Dombois and Fosberg 1998). Areas of exposed volcanic substrate are typically covered by grasslands

or sparsely forested savannas, especially in southern Guam, the Sabana region of Rota, and the central ridge of Saipan. These habitats are generally dominated by *Dimeria chloridiformis*, *Miscanthus floridulus*, or *Pennisetum polystachyon* (Mueller-Dombois and Fosberg 1998). On Tinian, nonforested areas are generally covered by invasive weeds, especially *Mimosa invisa* (Mueller-Dombois and Fosberg 1998).

Site Selection

Between April 2005 and June 2007, we sampled eight sites on Guam (one of which was sampled annually), four sites on Rota, five sites on Saipan, and three sites on Tinian (Table 1). On each island, we identified potential study sites based on habitat type and available area of relatively homogeneous habitat using 1:24,000 and 1:25,000 scale U.S. Geological Survey topographical maps and 1:20,000 scale vegetation maps (Falanruw et al. 1989). We selected sites in three major habitat types: native limestone forest (hereafter native forest), *L. leucocephala*-dominated forest (hereafter *Leucaena* forest), and grassland. Additional sites were selected near airports and seaports, which are critical areas for control and management efforts aimed at preventing Brown Tree Snake transport from Guam to other locations. These sites generally included a mixture of habitats (typically grassland and *Leucaena* forest) and were classified as mixed habitat. With the exception of mixed habitat, sites contained at least 4 ha of relatively homogeneous habitat. On each island, we sampled at least one native forest site, one grassland site, and one *Leucaena* forest site. Five sites were sampled near airports and seaports on Guam ($n = 2$), Rota ($n = 1$), and Saipan ($n = 2$) (Table 1).

TABLE 1

Introduced Small Mammal Sampling Coordinates and Dates on Guam, Rota, Saipan, and Tinian, 2005–2007

Site	Dates Sampled	Latitude	Longitude
Guam			
Grassland	6–10 June 2005	13.542	144.912
Leucaena forest 1	30 May–3 June 2005	13.512	144.870
Leucaena forest 2	20–24 June 2005	13.417	144.783
Leucaena forest 3	6–10 Nov. 2006	13.437	144.659
Leucaena forest 4	2–6 May 2005 15–19 May 2006 6–16 June 2007	13.640	144.865
Mixed	23–27 Oct. 2006	13.491	144.795
Native forest 1	18–22 Apr. 2005	13.648	144.863
Native forest 2	16–20 May 2005	13.378	144.672
Rota			
Grassland	23–27 Jan. 2006	14.140	145.191
Leucaena forest	30 Jan.–3 Feb. 2006	14.115	145.199
Mixed	10–14 Apr. 2006	14.170	145.240
Native forest	3–7 Apr. 2006	14.154	145.170
Saipan			
Grassland	19–23 Sep. 2005	15.238	145.773
Leucaena forest	26–30 Sep. 2005	15.108	145.729
Mixed 1	15–19 Aug. 2006	15.227	145.744
Mixed 2	22–26 Aug. 2006	15.127	145.727
Native forest	12–16 Sep. 2005	15.251	145.798
Tinian			
Grassland	24–28 Oct. 2005	14.951	145.651
Leucaena forest	7–11 Nov. 2005	15.076	145.640
Native forest	31 Oct.–4 Nov. 2005	15.043	145.629

Note: Coordinates indicate the centroid of each 1.56 ha site and are presented in decimal degrees (WGS 84, UTM Zone 55). Note that *Leucaena* forest 4 was sampled annually.

Small Mammal Sampling

The introduced small mammal community of the Mariana Islands consists of at least five species, ranging from the earliest introduction, *Rattus exulans*, which occurred no later than AD 1000–1200 (Steadman 1999), to the most recent introduction, *Suncus murinus*, first documented on Guam in 1953 (Peterson 1956). Other introductions include *Mus musculus*, first reported on Guam in 1819 (Freycinet 2003), and *R. norvegicus*, first reported on Saipan in the late 1800s (Kuroda 1938). Due to the uncertainty surrounding the identity of a third *Rattus* species, thought to be either *R. rattus* or *R. tanezumi*, two morphologically similar species only recently separated based on karyotypic differences (Musser and Carleton 2005), we collected genetic material from all captured *Rattus*. Preliminary genetic analysis (S. J. Oyler-McCance and J. St. John, unpubl. data) of randomly selected samples from Guam ($n = 17$), Rota ($n = 10$), Saipan ($n = 10$), and Tinian ($n = 10$) indicated that all were most closely related to the *R. diardii* group described by Robins et al. (2007). Until taxonomic identity of this group is resolved, we refer to them here as *R. diardii*.

At each site, we conducted mark-recapture livetrapping for five consecutive nights on an 11×11 grid with 12.5 m intervals between each trap station (1.56 ha). We placed a single standard-length folding Sherman live trap ($229 \times 89 \times 76$ mm [H. B. Sherman Traps, Inc., Tallahassee, Florida]) at each trap station ($n = 121$) and a single Haguruma wire mesh live trap ($285 \times 210 \times 140$ mm [Standard Trading Co., Honolulu, Hawai'i]) at every other trap station ($n = 36$). Trap selection and spacing were determined through preliminary testing and literature review of target species' home range and movement patterns, with the goal of maximizing captures. Sherman traps, which best captured *M. musculus* and *S. murinus* during preliminary testing, were spaced at 12.5 m intervals to match the relatively small home ranges of these species in the Mariana Islands (Baker 1946, Barbehenn 1969, 1974*a*). Haguruma traps, which best captured *Rattus* species during preliminary testing, were spaced at 25 m intervals to better match the larger home ranges of these species in the Mariana Islands (Baker 1946, Barbehenn 1969, 1974*a*).

We placed closed traps on the grid two nights before the beginning of sampling to provide an opportunity for small mammals to acclimate to their presence. Traps were placed on the ground and, whenever possible, positioned to provide shelter from sun and rain. Traps were baited with a mixture of peanut butter, oats, and food-grade paraffin and were checked beginning at 0730–0800 hours each day. Traps were closed during the day to minimize trap mortality, reopened at approximately 1600 hours, and rebaited as necessary.

We uniquely marked captured animals on each ear with numbered metal tags (*M. musculus* and *S. murinus*: small ear tags produced by S. Roestenburg, Riverton, Utah; *Rattus* species: no. 1005-1, National Band and Tag Co., Newport, Kentucky). We examined and measured captured animals to determine species, sex, age, reproductive status, mass (g), head-body length (mm), tail length (mm), right hind foot length (mm), right ear length (mm), and testes length (mm, if applicable). Capture, handling, and marking techniques followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) and the U.S. Geological Survey Animal Care and Use Committee (Fort Collins Science Center).

We also sampled each site (except for *Leucaena* forest 4 [Table 1]) with five consecutive nights of snaptrapping during the week following livetrapping. A comparison of livetrapping and snaptrapping will be published elsewhere; however, snaptrapping data were included in the calculation of body condition index and mean maximum distance moved. We also used snaptrapping data to evaluate the effectiveness of our livetrapping methodology. One concern with relatively short-duration sampling is that rare or nondominant species may not be captured (Brown et al. 1996, Harper and Veitch 2006). We documented only three instances (out of 43 possible) where species not captured during livetrapping were captured during snaptrapping. Twice, a single individual (one *M.*

musculus and one *R. diardii*) was captured and in the other instance five *S. murinus* were captured. Five of these seven captures occurred on the grid perimeter, suggesting snaptrapping-induced immigration (Stickel 1946) rather than species missed by livetrapping.

Data Analysis

We estimated density and biomass separately for each species. First, we generated site-specific estimates of abundance using estimated capture and recapture probability modeled from livetrapping data. Second, we estimated effective trapping area for each site with reference to each species' mean maximum distance moved between captures. Third, we calculated density as abundance/effective trapping area. Fourth, we determined site-specific mean body mass. Fifth, we calculated biomass as the product of site-specific density and mean body mass.

Data analysis followed an information-theoretic approach involving model selection and multimodel inference. Model selection was based on Akaike's Information Criterion corrected for small sample size (AIC_c [Burnham and Anderson 2002]). Models were considered competitive with the top-ranked model when $\Delta AIC_c \leq 2.0$ (Burnham and Anderson 2002). Model averaging was based on Akaike weights (w_i [Burnham and Anderson 2002]) and included the entire model set except for models with nonsensical β estimates (e.g., $\beta = 16.8$, $SE(\beta) = 2{,}084.6$). Unless otherwise indicated, estimates are presented as mean $\pm$ 1 SE.

MODELING CAPTURE AND RECAPTURE PROBABILITY. We generated model-averaged abundance estimates (Burnham and Anderson 2002) in Program MARK 4.3 (White and Burnham 1999) using the conditional likelihood closed capture-recapture model developed by Huggins (1989, 1991). This model uses estimates of capture probability and the number of individuals captured to estimate abundance and can account for heterogeneity in capture probability from temporal, behavioral, and individual effects (expressed as either unexplained heterogeneity (i.e., finite mixture distributions [Pledger 2000]) or covariate-associated capture heterogeneity [Huggins 1989, 1991]).

In Program MARK, we coded design matrices to allow sites to be treated both individually and as groups, based on common attributes such as island or habitat. Capture and recapture probability were primarily modeled across these groups to increase statistical efficiency (i.e., reduce estimate variance) and allow abundance estimates to be generated from sites with few captures or recaptures (Bowden et al. 2003). We specified models in an iterative fashion, beginning with models allowing capture probability to vary by time (t), behavior (b), individuals (i.e., capture heterogeneity, h), combinations of these factors, or constraining capture probability to be constant. We specified models incorporating capture heterogeneity as two-mixture models, based on concerns that our dataset would not support a more parameterized mixture model (Conn et al. 2006). If the top model included temporal variation, we fit a set of neophobia models to the dataset. Neophobia models allowed capture probability to vary during the first (neo1) or first and second (neo2) sampling occasions, while holding capture probability constant for the remaining occasions. Motivation for these models came from literature accounts of neophobia for *Rattus* (Temme and Jackson 1979, Inglis et al. 1996, Clapperton 2006). The next subset of models was parameterized to model capture probability, recapture probability, or both capture and recapture probability as a function of island, habitat, or site. We hypothesized that capture probability would differ between Guam (with brown tree snakes) and Rota, Saipan, and Tinian (without established Brown Tree Snake populations), so the island grouping was coded in two ways, with island[4] distinguishing each island and island[2] distinguishing Guam from the combination of Rota, Saipan, and Tinian.

Our final subset of models incorporated covariates, beginning with the global model and proceeding to more parsimonious models. Covariates under consideration included sex (male or female), age (adult or juvenile), reproductive status, body condition index,

body size, rain previous night, and rain amount. Reproductive status (repstat) was a categorical variable differentiating reproductively active adults from nonreproductive adults and juveniles; we assigned repstat class based on mass and the presence of externally visible sexual characteristics such as descended testes for males and active lactation for females. We calculated body condition index (bodycon) as the ratio between the observed and expected mass of an individual, where expected mass was determined from a linear regression of ln mass versus ln head-body length. For each species, we modeled variation in bodycon as a function of island[4], island[2], and habitat in an analysis of variance framework (Proc GLM [SAS Institute, Inc., Cary, North Carolina]). We then included bodycon estimates from the top model (or model-averaged bodycon) in covariate models. Body Size (size) was a species-specific composite variable created from a principal components analysis (Proc FACTOR [SAS Institute, Inc.]) of mass, head-body length, tail length, hind foot length, and ear length measured for each individual. We also included rain previous night (rainprev), a categorical measure of the presence or absence of rainfall during each trap night, and rain amount (rainamt), a quantitative measure of total rainfall (mm) at the center of each trapping grid. Our rainamt measurements encompassed a 24-hr period, with the exception of the first sampling occasion, for which rainamt included only the 12- to 16-hr period before trap monitoring. Before including rainamt, we determined that rainfall from the first sampling occasion did not differ appreciably from rainfall on other occasions based on overlapping 95% confidence intervals.

DENSITY AND BIOMASS ESTIMATION. For each site, we calculated species-specific density by dividing the model-averaged abundance estimates by effective trapping area, where effective trapping area equaled the total area encompassed by the trapping grid (1.56 ha) plus a boundary strip of half the mean maximum distance moved between captures for individuals captured two or more times (Wilson and Anderson 1985). For each species, variation in mean maximum distance moved was modeled as a function of island[4], island[2], and habitat in an analysis of variance framework (Proc GLM [SAS Institute, Inc.]). Mean maximum distance moved estimates from the top model (or model-averaged mean maximum distance moved) were used in density calculations. For each site, we calculated species-specific biomass as the product of density and mean body mass. We used the mean mass of individuals captured two or more times in calculations of species-specific mean body mass. We calculated the variance of density and biomass estimates using the delta method (Seber 2002).

RESULTS

We captured 707 *R. diardii*, 298 *S. murinus*, 154 *M. musculus*, 16 *R. exulans*, and five *R. norvegicus* in 17,270 trap nights. Of these, *R. diardii* was most common across habitats and islands (Table 2). In contrast, *S. murinus* was not captured on Rota (Table 3) and *M. musculus* was rarely captured at forested sites (Table 4). *R. exulans* and *R. norvegicus* were captured at only four sites each and will not be considered further. In general, captures of all species were greater on Rota, Saipan, and Tinian than on Guam.

Modeling Capture and Recapture Probability

R. diardii capture and recapture probability were best explained by an additive model ($w_i = 0.871$ [Table 5]) allowing neophobia (neo2) in capture probability for each island (island[4]), as well as capture probability variation by sex, repstat, and rainamt with recapture probability varying similarly by island[4], sex, repstat, and rainamt. Reproductively active females were more than twice as likely to be captured as nonreproductive males (Figure 1), and captures of all individuals increased with increasing rainfall. All plausible models contained the neo2 effect on capture probability; the top model without neo2 had no support ($\Delta AIC_c = 33.92$). All covariate effects were strong based on 95% confidence intervals that excluded zero.

Suncus murinus capture and recapture

TABLE 2

Number of Individuals (M_{t+1}) and Total (n.) *Rattus diardii* Captures, Density ($\hat{D}$ [animals/ha]) and Biomass Estimates ($\widehat{Biom}$ [kg/ha]), and Associated Standard Errors (SE) and 95% Confidence Intervals (95% CI) during Livetrapping in Grassland, *Leucaena* Forest, Mixed, and Native Forest Habitats on Guam, Rota, Saipan, and Tinian, 2005–2007

Site	M_{t+1}	n.	$\hat{D}$	SE	95% CI	$\widehat{Biom}$	SE	95% CI
Guam[a]								
Grassland	22	24	15.9	3.7	8.6–23.2	2.42	0.58	1.28–3.56
Leucaena forest 1	5	6	2.6	0.7	1.2–4.0	0.70	0.19	0.33–1.07
Leucaena forest 3	13	14	8.9	2.3	4.4–13.4	1.36	0.37	0.63–2.09
Leucaena forest 4[b]	4	4	2.6	1.0	0.6–4.6	0.39	0.16	0.08–0.70
	22	27	15.3	3.5	8.4–22.2	2.88	0.66	1.59–4.17
Mixed	1	1	0.7	0.5	0–1.7	0.06	0.05	0–0.16
Rota								
Grassland	88	119	73.2	11.9	49.9–96.5	9.80	1.62	6.62–12.98
Leucaena forest	42	63	36.0	6.7	22.9–49.1	4.63	0.89	2.89–6.37
Mixed	106	146	95.8	16.1	64.2–127.4	8.85	1.54	5.83–11.87
Native forest	11	11	9.2	2.2	4.9–13.5	1.03	0.28	0.48–1.58
Saipan								
Grassland	41	63	33.0	6.4	20.5–45.5	4.13	0.83	2.50–5.76
Leucaena forest	50	58	41.4	8.1	25.5–57.3	4.31	0.87	2.60–6.02
Mixed 1	29	34	25.1	5.4	14.5–35.7	3.03	0.68	1.70–4.36
Mixed 2	8	8	6.9	2.1	2.8–11.0	0.96	0.32	0.33–1.59
Native forest	24	28	21.6	5.1	11.6–31.6	3.18	0.76	1.69–4.67
Tinian								
Grassland	106	132	99.9	17.9	64.8–135.0	11.57	2.11	7.43–15.71
Leucaena forest	55	81	44.0	7.3	29.7–58.3	5.09	0.88	3.37–6.81
Native forest	80	92	75.1	13.6	48.4–101.8	8.78	1.63	5.59–11.97

[a] Zero *R. diardii* captured at three sites (one *Leucaena* forest and two native forest).
[b] Zero *R. diardii* captured during 2007 sampling at *Leucaena* forest 4.

TABLE 3

Number of Individuals (M_{t+1}) and Total (n.) *Suncus murinus* Captures, Density ($\hat{D}$ [animals/ha]) and Biomass Estimates ($\widehat{Biom}$ [kg/ha]), and Associated Standard Errors (SE) and 95% Confidence Intervals (95% CI) during Livetrapping in Grassland, *Leucaena* Forest, Mixed, and Native Forest Habitats on Guam, Saipan, and Tinian, 2005–2007

Site	M_{t+1}	n.	$\hat{D}$	SE	95% CI	$\widehat{Biom}$	SE	95% CI
Guam[a]								
Grassland	14	22	8.6	2.5	3.7–13.5	0.20	0.06	0.08–0.32
Saipan								
Grassland	19	41	13.4	3.7	6.1–20.7	0.24	0.08	0.08–0.40
Leucaena forest	43	63	31.6	10.2	11.6–51.6	0.88	0.27	0.35–1.41
Mixed 1	9	9	6.3	2.2	2.0–10.6	0.18	0.06	0.06–0.30
Mixed 2	47	59	32.9	9.6	14.1–51.7	0.98	0.28	0.43–1.53
Native forest	19	21	14.0	5.2	3.8–24.2	0.40	0.13	0.15–0.66
Tinian								
Grassland	11	11	8.9	2.5	4.0–13.8	0.16	0.05	0.06–0.26
Leucaena forest	93	113	73.7	20.1	34.3–113.1	1.87	0.52	0.85–2.89
Native forest	43	43	32.8	9.6	14.0–51.6	0.83	0.25	0.34–1.32

Note: S. murinus was neither captured nor observed on Rota.
[a] Zero *S. murinus* captured at seven sites (four *Leucaena* forest, one mixed habitat, and two native forest).

TABLE 4

Number of Individuals (M_{t+1}) and Total ($n.$) *Mus musculus* Captures, Density ($\hat{D}$ [animals/ha]) and Biomass Estimates ($\widehat{Biom}$ [kg/ha]), and Associated Standard Errors (SE) and 95% Confidence Intervals (95% CI) during Livetrapping in Grassland, *Leucaena* Forest, Mixed, and Native Forest Habitats on Guam, Rota, Saipan, and Tinian, 2005–2007

Site	M_{t+1}	$n.$	$\hat{D}$	SE	95% CI	$\widehat{Biom}$	SE	95% CI
Guam[a]								
Grassland	15	29	7.2	1.7	3.9–10.5	0.08	0.02	0.04–0.12
Rota								
Grassland	25	32	20.7	5.0	10.9–30.5	0.26	0.07	0.12–0.40
Leucaena forest	19	27	16.0	4.1	8.0–24.0	0.20	0.05	0.10–0.30
Mixed	32	51	26.5	6.3	14.2–38.8	0.34	0.08	0.18–0.50
Native forest	1	2	0.8	0.6	0–2.0	0.01	0.01	0–0.03
Saipan[b]								
Grassland	51	96	36.5	8.1	20.6–52.4	0.45	0.10	0.25–0.65
Leucaena forest	2	2	1.5	0.7	0.1–2.9	0.01	0.01	0–0.03
Tinian[c]								
Grassland	9	12	8.2	2.7	2.9–13.5	0.11	0.04	0.03–0.19

[a] Zero *M. musculus* captured at seven sites (four *Leucaena* forest, one mixed habitat, and two native forest).
[b] Zero *M. musculus* captured at three sites (two mixed habitat and one native forest).
[c] Zero *M. musculus* captured at two sites (one *Leucaena* forest and one native forest).

TABLE 5

Model Selection Results for Mark-Recapture Modeling of Capture (p) and Recapture (c) Probability for *Rattus diardii*, *Suncus murinus*, and *Mus musculus* Livetrapping Data Collected on Guam, Rota, Saipan, and Tinian, 2005–2007

	K	ΔAIC_c	w_i
Models for *R. diardii*			
$p_{neo2(island[4])+sex+repstat+rainamt}$ $c_{island[4]+sex+repstat+rainamt}$	16	0.00	0.871
$p_{neo2(island[4])+repstat+rainamt}$ $c_{island[4]+repstat+rainamt}$	15	5.72	0.050
$p_{neo2(island[4])+sex+age+repstat+bodycon+size+rainprev+rainamt}$ $c_{island[4]+sex+age+repstat+bodycon+size+rainprev+rainamt}$	20	6.97	0.027
$p_{neo2(island[4])+sex+rainamt}$ $c_{island[4]+sex+rainamt}$	15	7.12	0.025
$p_{neo2(island[4])+rainamt}$ $c_{island[4]+rainamt}$	14	7.56	0.020
$p_{neo2(island[4])+sex+repstat}$ $c_{island[4]+sex+repstat}$	15	9.61	0.007
Models for *S. murinus*			
p_{t+h} $c_{t(island[4])+h}$	10	0.00	0.994
$p_{t+h+sex+repstat+bodycon+size+rainprev+rainamt}$ $c_{t(island[4])+h+sex+repstat+bodycon+size+rainprev+rainamt}$	16	10.33	0.006
Models for *M. musculus*			
$p_{t(island[2])+h}$ c_{t+h}	11	0.00	0.349
$p_{t(island[2])+h}$ $c_{t(island[2])+h}$	13	0.10	0.331
$p_{t(island[4])+h}$ c_{t+h}	19	1.20	0.192
p_{t+h} $c_{t(island[2])+h}$	9	4.36	0.039
$p_{t(island[4])+h}$ $c_{t(island[4])+h}$	23	4.65	0.034
p_{t+h} c_{t+h}	7	5.01	0.029
p_{neo1+h} c_{h}	4	6.79	0.012
p_{t+h} $c_{t(habitat)+h}$	11	7.94	0.007
p_{neo2+h} c_{h}	5	8.82	0.004
$p_{t(island[2])+h+sex+repstat+bodycon+size+rainprev+rainamt}$ $c_{t+h+sex+repstat+bodycon+size+rainprev+rainamt}$	17	9.23	0.003

Note: Parenthetical terms indicate the nesting structure of the previous variable (e.g., neo2(island[4]) specifies separate two-day neophobia effects for each of four islands). All heterogeneity models (h) used two mixtures to approximate individual heterogeneity. Results include the number of model parameters (K), relative Akaike's Information Criterion corrected for small sample size (ΔAIC_c), and Akaike weight (w_i).

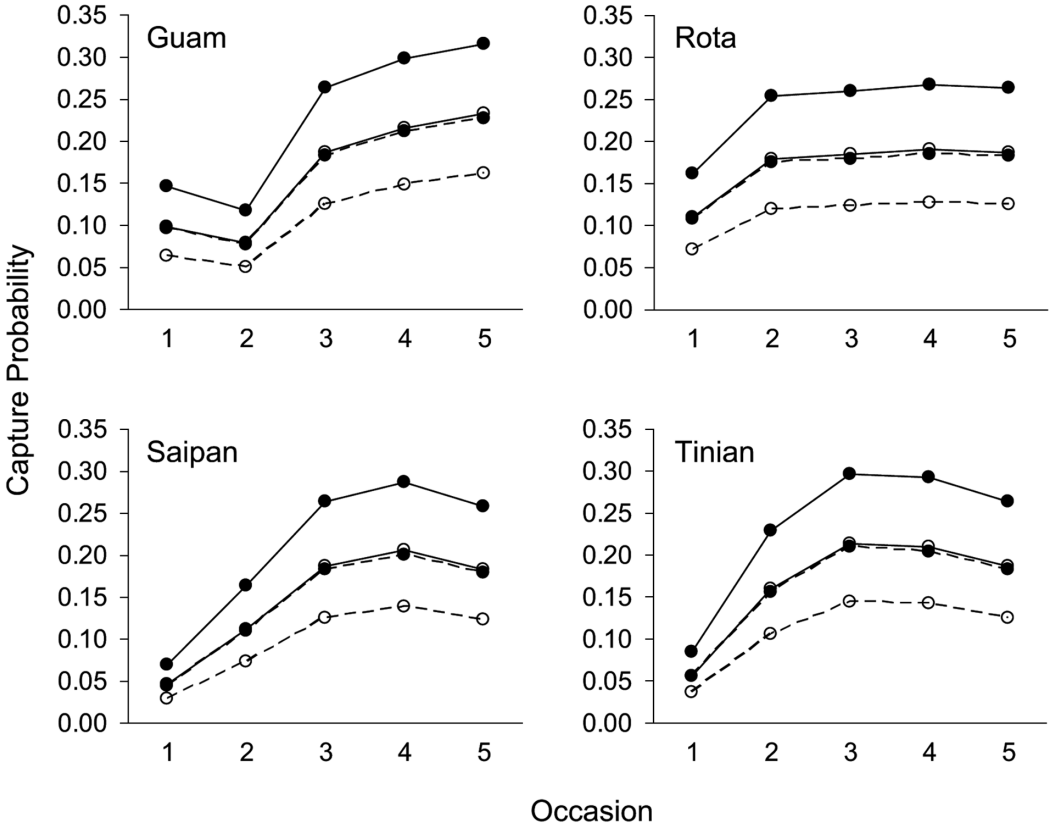

FIGURE 1. Effect of neophobia (reduced capture probability during occasions 1 and 2), sex (female, ●; male, ○), and reproductive status (reproductively active, solid line; nonreproductive, dashed line) on *Rattus diardii* livetrapping capture probability on Guam, Rota, Saipan, and Tinian, 2005–2007.

probability were best explained by an additive model allowing temporal variation and heterogeneity in capture probability and temporal variation for each island (island[4]) and heterogeneity in recapture probability ($w_i = 0.994$ [Table 5]). The top model without a temporal effect had no support ($\Delta AIC_c = 32.43$). Unexplained heterogeneity was approximated by two mixture classes composing 65% (low capture probability) and 35% (high capture probability) of the population; over half of the population had estimated daily capture probability < 0.16 (Figure 2).

M. musculus capture and recapture probability were best explained by three additive models allowing both temporal variation and heterogeneity in these parameters (Table 5). The top model without a temporal effect had no support ($\Delta AIC_c = 15.91$). Unexplained heterogeneity was approximated by two mixture classes composing 67.3% (low probability) and 32.7% (high probability) of the population. For Rota, Saipan, and Tinian, over half of the population had estimated daily capture probability < 0.20, whereas for Guam daily capture probability was generally higher (Figure 2).

Estimates of Maximum Mean Distance Moved

Rattus diardii mean maximum distance moved varied between islands (island[4]; $w_i = 0.977$) and was greatest on Guam (35.6 ± 5.4 m; $n = 33$), followed by Saipan (22.8 ± 2.5 m;

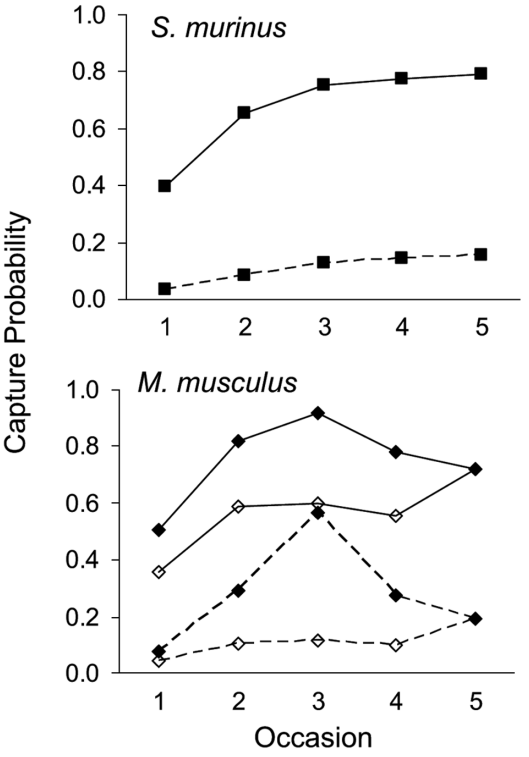

FIGURE 2. *Suncus murinus* and *Mus musculus* mixture-specific capture probability during livetrapping conducted on Guam, Rota, Saipan, and Tinian, 2005–2007. For *S. murinus* (■), the high mixture class (solid line) composed 35% of the population, whereas the low mixture class (dashed line) composed 65% of the population. *Mus musculus* mixture-specific capture probabilities differed between Guam (◆) and the combination of Rota, Saipan, and Tinian (◇), with the high mixture class (solid line) composing 32.7% of population and the low mixture class (dashed line) composing 67.3% of the population.

$n = 100$), Rota (14.5 ± 1.6 m; $n = 175$), and Tinian (14.5 ± 1.3 m; $n = 180$). *Suncus murinus* mean maximum distance moved varied between habitats ($w_i = 0.987$) and was greatest in grassland (29.2 ± 2.7 m; $n = 48$), followed by mixed habitat (19.3 ± 3.2 m; $n = 25$), *Leucaena* forest (16.3 ± 1.4 m; $n = 68$), and native forest (14.2 ± 3.5 m; $n = 12$). *Mus musculus* mean maximum distance moved varied between islands (island[4]; $w_i = 0.718$), although there was also support for the simpler island model (island[2]; $w_i = 0.272$). Model-averaged mean maximum distance moved was greatest on Guam (31.2 ± 3.6 m; $n = 25$), followed by Saipan (22.8 ± 2.5 m; $n = 77$), Rota (18.2 ± 3.2 m; $n = 59$), and Tinian (11.7 ± 8.7 m; $n = 3$).

Density Estimates

Mean *R. diardii* density was greatest on Tinian (73.0/ha), followed by Rota (53.5/ha) and Saipan (25.6/ha), with much lower values on Guam (5.1/ha) (Table 2). Mean *S. murinus* density was also much greater on Tinian (38.5/ha) and Saipan (19.6/ha) than on Guam (1.0/ha) (Table 3). Mean *M. musculus* density was greatest on Rota (15.8/ha), followed by Saipan (7.7/ha), Tinian (2.6/ha), and Guam (0.8/ha [Table 4]).

Biomass Estimates

For each species, mean biomass was greater on Rota, Saipan, and Tinian than on Guam (Tables 2–4). On Rota, Saipan, and Tinian, *R. diardii* and *M. musculus* biomass were greatest in grassland (Figure 3), with maximum estimates of 11.6 kg/ha and 0.4 kg/ha, respectively. In contrast, *S. murinus* biomass was highest in *Leucaena* forest on Saipan and Tinian (Figure 3), with a maximum estimate of 1.9 kg/ha. On Guam, mean biomass was greatest in grassland for all species, although moderate levels of *R. diardii* biomass were also observed in *Leucaena* forest (Figure 3).

DISCUSSION

We documented high but variable introduced small mammal density and biomass on the islands of Rota, Saipan, and Tinian. Maximum *R. diardii* density estimates on these islands were two to three times greater than historic *Rattus* estimates from Guam or other tropical Pacific islands, including Pohnpei (4.0–8.5/ha [Strecker 1962]), Majuro (11.3/ha [Strecker 1962]), and Eniwetok (19.9/ha [Jackson 1967]). The high densities observed during our study, especially on Rota and Tinian, could indicate population irruptions. We speculate, however, that our observation of high densities across habitats, islands, and

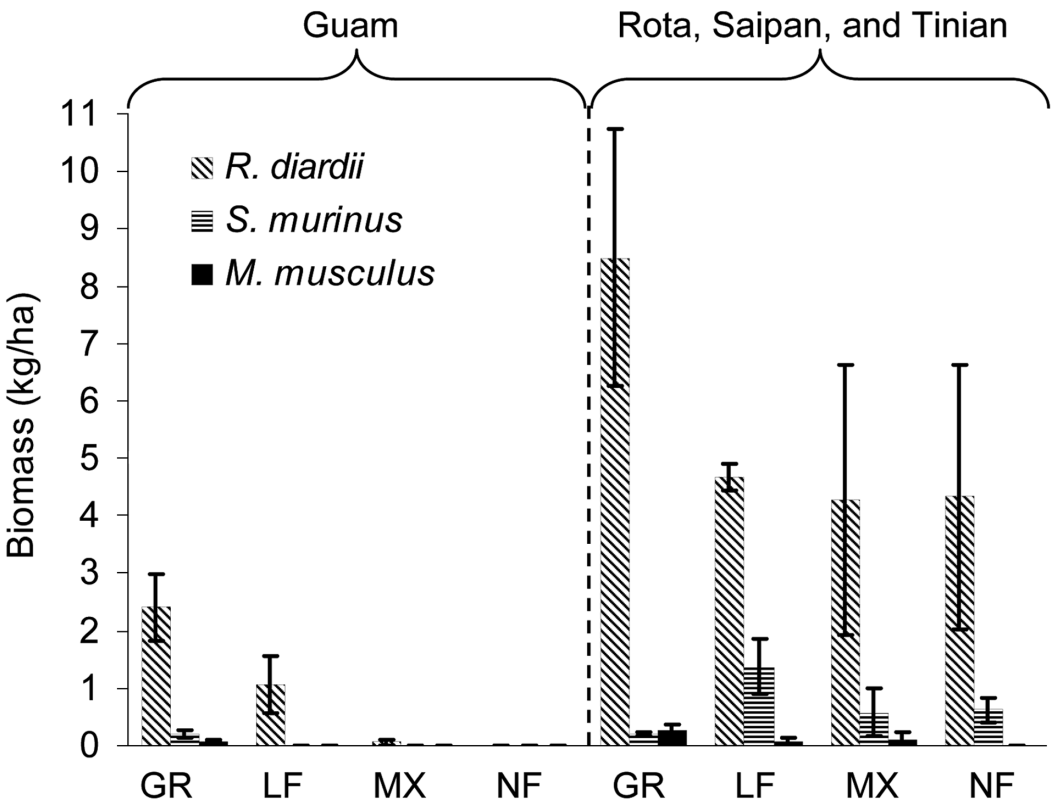

FIGURE 3. Mean *Rattus diardii*, *Suncus murinus*, and *Mus musculus* biomass estimates derived from mark-recapture live-trapping of grassland (GR), *Leucaena* forest (LF), mixed (MX), and native forest (NF) habitats on Guam, Rota, Saipan, and Tinian, 2005–2007. Bars indicate ± 1 SE.

time represent persistent high-density populations. Comparable densities have been recorded for a smaller introduced *Rattus* species (*R. exulans*) on small, relatively competitor- and predator-free islands. On Kure Atoll, Wirtz (1972) documented mean *R. exulans* density of 111.2/ha during sampling from March 1964 to May 1965, with monthly estimates of 49.4–185.3/ha. Similarly, on Tiritiri Matangi Island, New Zealand, Moller and Craig (1987) estimated peak *R. exulans* densities of 130 ± 20/ha in grassland and 101 ± 12/ha in forest during regular sampling from February 1975 to May 1977. Using mass data provided in Wirtz (1972) and Moller and Craig (1987), these densities translate to biomass of ca. 3.4–8.9 kg/ha on Kure Atoll and peak biomass of 9.9 and 6.9 kg/ha in grassland and forest, respectively, on Tiritiri Matangi Island.

Our *R. diardii* density and biomass estimates were considerably lower on Guam and were also lower than Guam *Rattus* estimates from 1945 (10.9–30.0/ha [Baker 1946]) and the early 1960s (18.8/ha [Barbehenn 1969, 1974*b*]). Our Guam estimates were generally lower in forest than in grassland, a pattern first observed in the 1980s by Savidge (1986; forest: 0–2.5/ha, grassland: 36.4/ha). Gragg (2004) also found high *Rattus* density (14.7–69.8/ha) in grassland in 2002–2003. This pattern is at least partially attributable to variable Brown Tree Snake predation pressure, because snake density is generally greatest in forest on Guam (Savidge 1987, 1991).

Although *S. murinus* was reported on Rota

in 1966 (Barbehenn 1974*b*), we neither captured nor observed this species during 9 weeks on the island. On Saipan and Tinian, *S. murinus* density and biomass were generally greatest in *Leucaena* forest, whereas we had zero captures at forest sites on Guam, perhaps due to Brown Tree Snake predation pressure in that habitat. In general, our estimates of *S. murinus* density are comparable with historic values from Guam (25.4/ha [Barbehenn 1969, 1974*b*]; 19.1/ha [Savidge 1986]) and more recent estimates from Saipan (16.7–27.3/ha [S. Vogt, unpubl. data]). Our estimates are also similar to values obtained on Ile aux Aigrettes (29.2/ha) and Ile de la Passe (20/ha), two islands off the coast of Mauritius in the Indian Ocean (Varnham et al. 2002). However, our maximum density of 73.7/ha greatly exceeds known values and could indicate an irruptive potential for this species in the Mariana Islands.

Mus musculus was most common in grassland and mixed-habitat sites with patchy vegetation and exposed soil. Baker (1946:398) noted a similar preference for "open grass and brush land" and areas where "limestone soils are exposed" on Guam. Our *M. musculus* density estimates are comparable with historic values (8.3–25.8/ha [Baker 1946]) but less than more-recent estimates from Guam (18.5–104.0/ha [Gragg 2004]). Our estimates may have been influenced by *R. diardii* activity (Brown et al. 1996). To investigate this possibility, we added site-specific *R. diardii* density as both a linear and quadratic function to the top *M. musculus* model. There was limited support for the linear model ($\Delta AIC_c = 0.21$), indicating that *R. diardii* density had a weak negative effect on *M. musculus* capture probability ($\beta = -0.008 \pm 0.006$ [logit scale], 95% CI = −0.019–0.003).

When interpreting our density and biomass estimates, it is critical to recognize the potential for site-specific temporal variability. Annual sampling over 3 yr at a single site on Guam (*Leucaena* forest 4) revealed significant temporal variation in *R. diardii* density and biomass, which increased from 2.6/ha and 0.4 kg/ha, respectively, in 2005 to 15.3/ha and 2.9 kg/ha in 2006. In 2007, 10 days of livetrapping (1,570 trap nights) yielded zero captures. Sampling occurred at the same time each year (early May–early June) and therefore represents annual variability, as opposed to intra-annual variability, which was not examined during this study.

Modeling Capture and Recapture Probability

By modeling the effects of temporal variation, spatial variation, and heterogeneity on capture and recapture probability, we were able to generate robust and reliable estimates of density and biomass. Knowledge of these effects may also prove beneficial for planning future sampling and data analysis.

TEMPORAL VARIATION. We documented lower capture probability for *R. diardii* on the first and second occasion, likely due to neophobia. Neophobia has been observed in laboratory, commensal, and wild *Rattus* populations (Temme and Jackson 1979, Inglis et al. 1996, Clapperton 2006). *Suncus murinus* capture probability also increased over time, suggesting neophobia, although this effect was not strongly supported in models. Although some researchers have documented a similar response (e.g., fig. 6 in Seymour et al. [2005]), the general consensus is that *S. murinus* is neophilic and likely to investigate, rather than avoid, new objects (Churchfield 1990). The pattern of temporal variation was less clear for *M. musculus*, although there was an indication of increasing capture probability over time on Rota, Saipan, and Tinian. Extended trap acclimation (greater than 2 nights) or prebaiting might reduce temporal variation in capture probability.

SPATIAL VARIATION. For each species, we documented capture or recapture probability variation by island, potentially due to a combination of differing land-use histories and ungulate and predator densities. Each island has experienced substantial but variable disturbance as a result of military activities and loss of native habitats to agriculture and development. The vegetative community has also been modified by introduced ungulates, including feral pigs (*Sus scrofa*) and Philippine deer (*Cervus mariannus*) on Guam, Rota, and

Saipan (Stinson 1994, Vogt and Williams 2004, Wiles 2005) and domestic cattle (*Bos taurus*) on Tinian (Wiles et al. 1990). In addition to the Brown Tree Snake on Guam, each island is home to a variety of potential predators, including feral cats (*Felis catus*) and dogs (*Canis familiaris*) and monitor lizards (*Varanus indicus* [Stinson 1994, Fritts and Rodda 1998, Vogt and Williams 2004, Wiles 2005]).

HETEROGENEITY. The addition of covariates improved the precision of site-specific *R. diardii* abundance estimates by an average of 25.7% (range: 8.1%–57.2%). The importance of sex (female > male) and reproductive status (reproductively active > nonreproductive) suggests that social structure and dominance influenced capture and recapture probability. These results are consistent with those of Ewer (1971), who found that female *R. rattus* were more aggressive than males and adults were generally dominant over juveniles. We speculate that the positive relationship between rainfall and capture probability resulted from increased activity as individuals searched for standing water after rainfall events. The limestone substrate of the Mariana Islands is highly permeable, and available surface water is typically rare or nonexistent (Mueller-Dombois and Fosberg 1998). Thus, other than the moisture available in food items, surface water may be limited except immediately after rainfall. For *S. murinus* and *M. musculus*, heterogeneity in capture and recapture probability was accounted for with two-mixture models, rather than covariates. Other researchers have documented heterogeneity in capture probability for *S. murinus* (Seymour et al. 2005) and *M. musculus* (Conn et al. 2006).

Implications for Ecology in the Mariana Islands

Although the negative effects of introduced small mammals on island ecology are well documented (Atkinson 1985, Towns et al. 2006, Jones et al. 2008), little direct evidence exists for the Mariana Islands. However, it is likely that the high-density populations documented during our research have negative effects on native species in the Mariana Islands (Fritts and Rodda 1998). In recent years, researchers have noted apparent declines of several avian species, including the bridled white-eye (*Zosterops conspicillatus rotensis* [Fancy and Snetsinger 2001]) and Mariana crow (*Corvus kubaryi* [Plentovich et al. 2005, U.S. Fish and Wildlife Service 2005]) on Rota and the Micronesian megapode (*Megapodius laperouse*) and Mariana fruit dove (*Ptilinopus roseicapilla*) on Saipan (Craig 1999). The potential role of introduced small mammals in recent declines is often disregarded because *R. exulans* has been present in the Mariana Islands for at least 1,000 yr (Steadman 1999). However, *R. exulans* is generally considered less detrimental to birds than other introduced *Rattus* species (Atkinson 1985, Thibault et al. 2002, Towns et al. 2006, Jones et al. 2008). More important, the impact of *R. diardii* on birds in the Mariana Islands is unclear at this time. Further, temporal shifts in the abundance or distribution of *Rattus* species may obscure their role in avian declines. High-density introduced small mammal populations on Rota, Saipan, and Tinian might also impact avian species through dietary competition. Competition for invertebrate and reptilian prey could be especially problematic for nesting birds, because these high-protein items are required for nestlings.

Introduced *Rattus* species have also been implicated in invertebrate and reptilian declines (Whitaker 1973, Towns et al. 2006, Hoare et al. 2007), although the insectivorous *S. murinus* may be more problematic for these taxa in the Mariana Islands. This species has been implicated in the decline of invertebrates and reptiles on Mauritius and nearby islands (Varnham et al. 2002). On Guam, Barbehenn (1974*b*) observed no skinks during the peak of the *S. murinus* irruption in the early 1960s, which contrasts with the current abundance and visibility of skinks on Guam. More recently, Fritts and Rodda (1998) documented large differences in skink density between Saipan, where *S. murinus* was common (2,200 skinks/ha), and areas on Guam with few *S. murinus* (8,850 skinks/ha). Similarly, Rodda and Fritts (1992) implicated *S. murinus* in the decline of the pelagic gecko (*Nactus*

pelagicus), which was common on Rota, where *S. murinus* was absent, but uncommon or possibly extinct on Guam, Saipan, and Tinian, where *S. murinus* was historically or currently abundant.

Implications for Brown Tree Snake Control and Management

Introduced small mammals have important impacts on the effectiveness of Brown Tree Snake control efforts, which are highly dependent on traps using live, domestic mice (*M. musculus*) as attractants. These traps are placed around airports, seaports, and other cargo-handling facilities on Guam, as well as in locations vulnerable to accidental brown tree snake introductions, such as Rota, Saipan, and Tinian. Mouse-attractant traps are also commonly deployed in response to snake sightings in Brown Tree Snake–free locations. However, recent research suggests that Brown Tree Snake trap capture rates are inversely related to small mammal density. For example, Rodda et al. (2001) found a strong correlation ($R^2 = 0.90$) between Brown Tree Snake capture rates and indices of small mammal density and documented a sevenfold increase in Brown Tree Snake capture rates in areas of very low small mammal density on Guam. Similarly, Gragg et al. (2007) documented a 22%–65% increase in Brown Tree Snake capture probability after reducing small mammal density with localized rodenticide application. Our small mammal density estimates suggest reduced effectiveness of mouse-attractant traps on Rota, Saipan, and Tinian. Further, the majority of Brown Tree Snake control and eradication tools currently being developed, such as acetaminophen delivery devices (Savarie et al. 2001), also rely on mouse-based attractants and will likely be subject to the same reduced effectiveness in areas of high small mammal density.

A second, though perhaps less obvious, effect of introduced small mammals on Brown Tree Snake control and management relates to their impact on island trophic systems and predator-prey relationships. On Guam, introduced prey species, including small mammals, skinks, and geckos, were abundant and widespread at the time of Brown Tree Snake introduction (Baker 1946, Fritts and Rodda 1998). Because these species evolved with predators, they were better able to persist under Brown Tree Snake predation than the predator-naive species native to Guam. These introduced prey species facilitated and supported a high-density Brown Tree Snake population, even as native avian and reptilian species declined (Fritts and Rodda 1998), a phenomenon known as hyperpredation (Courchamp et al. 2000). By the time Brown Tree Snake predation pressure began to reduce introduced prey densities (forcing a decline in Brown Tree Snake density), many native species were already extinct. The high-density introduced small mammal populations documented on the islands of Rota, Saipan, and Tinian during our study suggest that a similar scenario could develop should a Brown Tree Snake population become established on those islands.

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